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Research Article

Differences in antennal morphology and body size might offset increased overlap in food particle size among invasive Ponto-Caspian corophiids (Crustacea, Amphipoda)

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Abstract

After *Chelicorophium curvispinum*, *C. sowinskyi*, and *C. robustum*, recently the fourth Ponto-Caspian filter feeding corophiid (*C. maeoticum*) has colonized the lower section of the River Rhine in the Netherlands. To test for niche differentiation among the four species along the food particle size spectrum, we measured their filter mesh sizes (i.e., the distance between bristles on the filtering setae). For comparison, we also analyzed a historic sample from the River Tisza in Hungary in which *C. maeoticum* co-occurred only with *C. sowinskyi*. We also compared the relative lengths and widths of the second antennae among the species, considering the potential involvement of this appendage in interference competition and deposit feeding. Despite significant interspecific differences in filter mesh sizes in most comparisons, there was a partial overlap between *C. maeoticum* and *C. sowinskyi* in the River Rhine but not in the River Tisza. In addition, there was an almost complete overlap between *C. curvispinum* and *C. robustum*. Marked interspecific differences could be observed in the relative widths of the second antennae in both sexes, potentially related to performance in competition for microhabitats. Remarkably, the earlier colonists *C. curvispinum* and *C. sowinskyi* have thinner second antennae while *C. robustum* and *C. maeoticum* with more robust appendages could establish in habitats already occupied by their congeners. Our results suggest that competition for both food and space can shape the coexistence and invasion patterns of Ponto-Caspian corophiids. Nevertheless, more studies are needed to reveal the range of behaviors second antennae are involved in and how their morphological features determine their functionality. The observed differentiation in the measured traits along with differences in body sizes close to the 1.3 ratio are likely to allow the coexistence of the four species and portend the continued spread of *C. maeoticum*.

Key words: Coexistence, filter feeding, filter mesh size, interference competition, niche differentiation

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Introduction

The Ponto-Caspian region, encompassing the Black, Azov, Caspian, and Aral Sea basins, is one of the most important source areas of aquatic invasive species across Europe and North-America (Ricciardi and MacIsaac 2000; Copilaș-Ciocianu et al. 2023). The colonization success of numerous Ponto-Caspian endemics is often cited as an example of an 'invasional meltdown', suggesting that previous invaders promote the establishment of additional ones through facilitative interactions,

such as provision of food or shelter (Ricciardi 2001). Nevertheless, such interactions can form only between functionally dissimilar species with different trophic positions (predator vs. prey) and/or habitat use (dreissenid mussels vs. gammarid amphipods), whereas the dominant interaction among functionally similar species with overlapping fundamental niches is inherently competitive. Since the majority of the endemic Ponto-Caspian fauna belongs to relatively few but diverse functional groups (e.g., Copilaș-Ciocianu and Sidorov 2022; Grabowska et al. 2023), new colonizers often face competition with already established species. Due to their shared evolutionary history, the species have developed mechanisms of niche differentiation which allows their coexistence within their native ranges on certain spatial scales (Borza et al. 2018b). However, it is not evident that those factors are also present in their novel environments, implying that recipient communities might become saturated before the species pool in the source region gets exhausted. While failed invasions are likely to remain unnoticed, several cases of new invaders displacing earlier colonists are reported; e.g., among *Dikerogammarus* and *Dreissena* species (Karatayev et al. 2015; Borza et al. 2017a).

Corophiid amphipods ('mud shrimp') are one of the groups which diversified in the Ponto-Caspian region with several endemic species belonging to the *Chelicorophium* genus (Bousfield and Hoover 1997; Uryupova and Mugue 2007). Since the early 20th century, three species have expanded their ranges across Europe. *C. curvispinum* (G.O. Sars, 1895) was the first to reach Western Europe from Poland via the 'central corridor', while the spread of *C. robustum* (G.O. Sars, 1895) and *C. sowinskyi* (Martynov, 1924) was facilitated mainly by the opening of the Main-Danube canal in the 1990s (Bij de Vaate et al. 2002; Borza et al. 2010). Recently a fourth species, *C. maeoticum* (Sowinsky, 1898) was also recorded in the Netherlands, likely arriving directly by sea freighters, not through the interconnected inland waterways (Wiggers and van Megen 2022). Since its discovery in 2021, it has colonized all major stretches of the Rhine system, large lakes (Ijsselmeer, Markermeer), as well as the inland canal system (unpublished data; Rijkswaterstaat, Eurofins AquaSense, Waardenburg Ecology). Although it was considered among potential future invaders due to its preference for hard substrates, the risk of its range expansion was regarded as low due to its apparent rarity within its native range compared to the three already invasive *Chelicorophium* species (Borza et al. 2017b, 2021b). What made its invasion even more surprising is the fact that its range narrowed in the River Danube basin during the 20th century (Borza et al. 2015).

Corophiids are filter or deposit feeders living in their self-constructed tubes in the sediment or among stones (Riisgård and Schotge 2007). Under hypertrophic conditions and low predation pressure, they can reach densities of over 100,000 specimens per m^2 at which their tubes create a thick layer of mud, depriving other sedentary animals of substrates or even suffocating them (Van den Brink et al. 1993). Although their densities are usually much lower than that, they still have an important ecological function as filter feeders and food sources for various predators.

The mesh size of their filtering screens formed by bristled setae on their second gnathopods is a crucial trait for corophiids since food particle size is a major factor in their niche differentiation, allowing the local coexistence of multiple species (Borza et al. 2018c). While coevolved species tend to differentiate along this niche axis, the high overlap in filter mesh size between the invasive *C. curvispinum* and the native *Apocorophium lacustre* (Vanhöffen, 1911) might have contributed to

the decline of the latter in coastal areas of the Baltic and North Sea (Borza et al. 2021a). Previous studies have demonstrated that corophiids can divide the food particle size spectrum into three parts (Borza et al. 2018c, 2021a), questioning whether the four invasive *Chelicorophium* species can coexist locally.

Nonetheless, it has also become evident that additional niche axes can decrease the intensity of competition among the species. Differentiation along the salinity gradient and between substrate types allowed the coexistence of the native Baltic corophiids with *C. curvispinum* on a broader spatial scale (Borza et al. 2021a). However, separation along environmental factors was not observed among the three invasive Ponto-Caspian species in the River Danube (Borza et al. 2018c). Differences in body size can also likely contribute to local species coexistence between *C. curvispinum* and *C. robustum* (Borza 2021) as well as between *Corophium volutator* (Pallas, 1766) and *Corophium arenarium* Crawford, 1937 (Jensen and Kristensen 1990). In the latter case, interference competition for burrows was suggested to take place between the species, where the individuals fight each other using their enlarged second antennae. This behavior has also been observed in fights between males over females in *C. volutator* (Meadows and Reid 1966). Besides their role in aggressive interactions, the second antennae are also used for scraping the sediment surface around the openings of the burrows during deposit feeding in *C. volutator* (Meadows and Reid 1966; Riisgård and Schotge 2007). Although deposit feeding has not been demonstrated in the invasive Ponto-Caspian corophiids, if present, it could provide an additional opportunity for differentiation among the species, contributing to their coexistence.

In this study, we aimed to test for morphological differentiation among the four invasive Ponto-Caspian *Chelicorophium* species to assess which niche axes might determine their coexistence. First, we measured the filter mesh sizes of the four species in materials from the estuarine section of the River Rhine in the Netherlands where they co-occur. For comparison, we also analyzed a historic sample from the River Tisza in Hungary in which *C. maeoticum* co-occurred only with *C. sowinskyi* and has disappeared since. In addition, we measured the relative lengths and widths of the second antennae of the four species to test for the potential role of interference competition and deposit feeding in the coexistence of the species. We also discuss how differences in the maximal body sizes of the species can modulate their interactions.

Methods

Morphological measurements

The analyzed material from the Netherlands was collected in different river stretches of the Lower Rhine and the Rhine Delta (Table 1, Fig. 1). The sample from the River Tisza represents the most upstream known occurrence of *C. maeoticum* in the River Danube basin (Table 1, Fig. 1), stored in the Hungarian Natural History Museum (accession no. 2344 and 3549; Borza 2011). The species later apparently disappeared from the River Tisza while *C. sowinskyi* – co-occurring with *C. maeoticum* in the sample – is still present along with *C. curvispinum*, and recently it was also joined by *C. robustum* (Borza et al. 2021b). The Museum authorized the dissection of four *C. maeoticum* specimens out of the 10 in the sample for the measurement of filter mesh sizes in the present study. The filter mesh sizes of the co-occurring *C. sowinskyi* specimens were already analyzed in the study by Borza (2021).

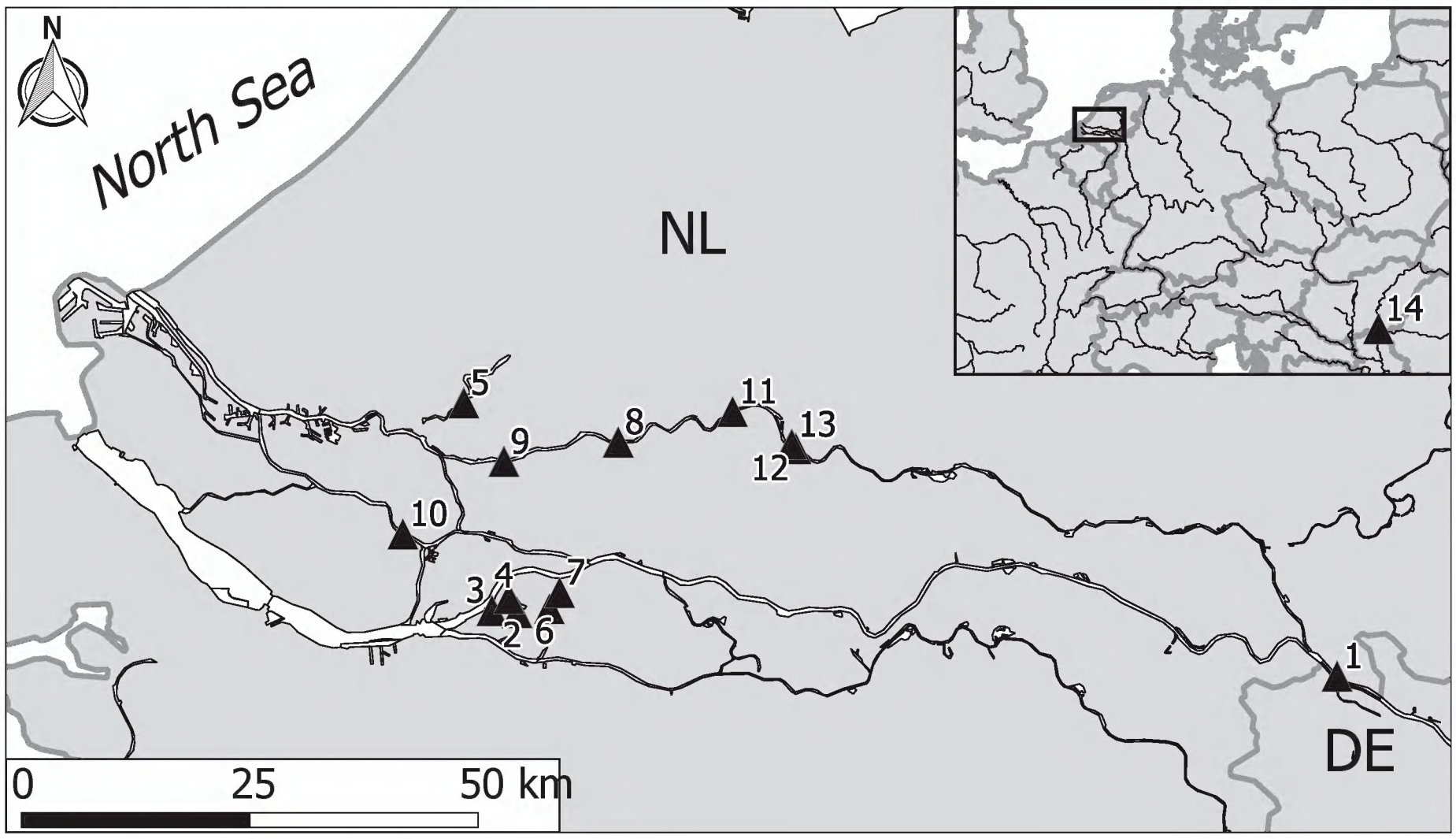

Figure 1. Map of the sampling sites. Site numbers as in Table 1.

Table 1. The material analyzed in the study. The numbers of specimens are indicated as: all (females, males, juveniles). Abbreviations: CC = *C. curvispinum*, CM = *C. maeoticum*, CR = *C. robustum*, CS = *C. sowinskyi*.

Site	Date	Waterbody	Coordinates	Method	Material			
					CC	CM	CR	CS
1	16/04/2024	River Rhine	51°51'16.0"N, 6°05'29.4"E	Bag of stones	8(3,5,0)	3(2,1,0)	3(2,1,0)	
2	22/04/2024	Gat van Kampen	51°45'17.1"N, 4°47'21.3"E	Boxcorer	8(6,2,0)	3(0,3,0)	8(7,1,0)	4(3,1,0)
3	22/04/2024	Gat van Den Kleinen Hil	51°45'06.4"N, 4°44'58.2"E	Littoral stones (brushing)	1(0,1,0)	11(6,5,0)	1(1,0,0)	2(0,2,0)
4	22/04/2024	Gat van Den Kleinen Hil	51°46'00.3"N, 4°46'18.4"E	Littoral stones (brushing)	3(0,3,0)	16(7,9,0)		9(6,3,0)
5	23/04/2024	Hollandsche Ijssel	51°56'41.8"N, 4°38'11.0"E	Littoral stones (brushing)		3(1,2,0)		
6	23/04/2024	Noordwaard	51°45'54.2"N, 4°50'19.1"E	Van Veen grab	1(0,1,0)	2(0,2,0)		4(3,1,0)
7	23/04/2024	Noordwaard	51°46'58.3"N, 4°50'56.9"E	Van Veen grab		1(1,0,0)		26(13,13,0)
8	25/04/2024	River Lek	51°56'20.4"N, 4°53'28.9"E	Van Veen grab		4(1,3,0)		
9	25/04/2024	River Lek	51°53'48.7"N, 4°43'07.6"E	Van Veen grab		11(7,4,0)		
10	25/04/2024	Oude Maas	51°48'24.3"N, 4°35'06.6"E	Van Veen grab		10(2,8,0)		
11	25/04/2024	River Lek	51°59'28.5"N, 5°03'38.0"E	Littoral stones (brushing)		10(3,7,0)		
12	25/04/2024	River Lek	51°58'06.3"N, 5°10'18.8"E	Handheld vacuum cleaner	10(6,4,0)		4(1,3,0)	1(0,1,0)
13	25/04/2024	River Lek	51°58'17.8"N, 5°09'50.0"E	Littoral stones (brushing)	6(2,4,0)	8(1,7,0)	3(2,0,1)	
14	9–10/1943	River Tisza (Hungary)	46°15'01.4"N, 20°09'12.1"E	n.a.		4(3,0,1)		25(11,10,4)

The measurement of filter mesh sizes conformed to the method of previous studies (Borza et al. 2018c, 2021a; Borza 2021). After the measurement of body length by ocular micrometer and the determination of sex, one of the second gnathopods of the specimens was dissected and the medial row of filtering setae removed under stereomicroscope. The preparations were mounted on slides with glycerol and photographed under light microscope (Zeiss AxioLab A1). Ten measurements per individuals were made (each on different setae near the basis) spanning six bristles (i.e., five gaps) in ImageJ2. Filter mesh sizes, i.e. distances between adjacent bristles were obtained by dividing the measured distances by five.

The measurement of the length and width of the second antennae was made on adult specimens from the Dutch samples, supplemented by specimens from the German section of the River Rhine analyzed by Borza (2021; samples 29–30) in the case of *C. robustum* (N = 10 per species and sex, except for *C. robustum* males, where N = 7). After the measurement of body length and the determination of sex, one of the second antennae was detached from the specimens between the 2nd and 3rd segments (corresponding to the flexible part of the limb), and placed on the bottom of the dish on its medial side. The width of the antenna was measured at the center of the 3rd segment (Fig. 2,'W'), whereas the length was measured in three parts by ocular micrometer since the preserved antennae usually cannot be extended into a linear position without damage (Fig. 2, 'L1-L2-L3'). As the borders between the segments were usually not clearly visible in the central part of the limbs, the dorsal breakpoints between the segments were used as endpoints for the measurements (Fig. 2).

Statistical analysis

The intra- and interspecific variation of filter mesh sizes was modelled in linear mixed-effect models in the package 'nlme' (Pinheiro and Bates 2000; Pinheiro et al. 2025) in R 4.5.1 (R Core Team 2025). Since exploratory analyses indicated an exponential body length dependency of the within-individual variation in filter mesh sizes, a variance term ('varExp') was included in all models. Models of intraspecific variation for all four species separately in the Dutch material featured sex, body length, and their interaction as fixed effects and individuals in sampling sites as hierarchical random effects (intercepts). Models of interspecific variation for the Dutch and Hungarian materials separately included species, body length and their interaction as fixed effects and individuals as random effects (intercepts). The optimal combinations of fixed effects were identified by the stepwise elimination of non-significant variables (Suppl. material 1: table S1). Pairwise comparisons between the intercepts of the species with Tukey's correction for comparing a family of four estimates in the Dutch material were made using the 'emmeans' package (Lenth 2025).

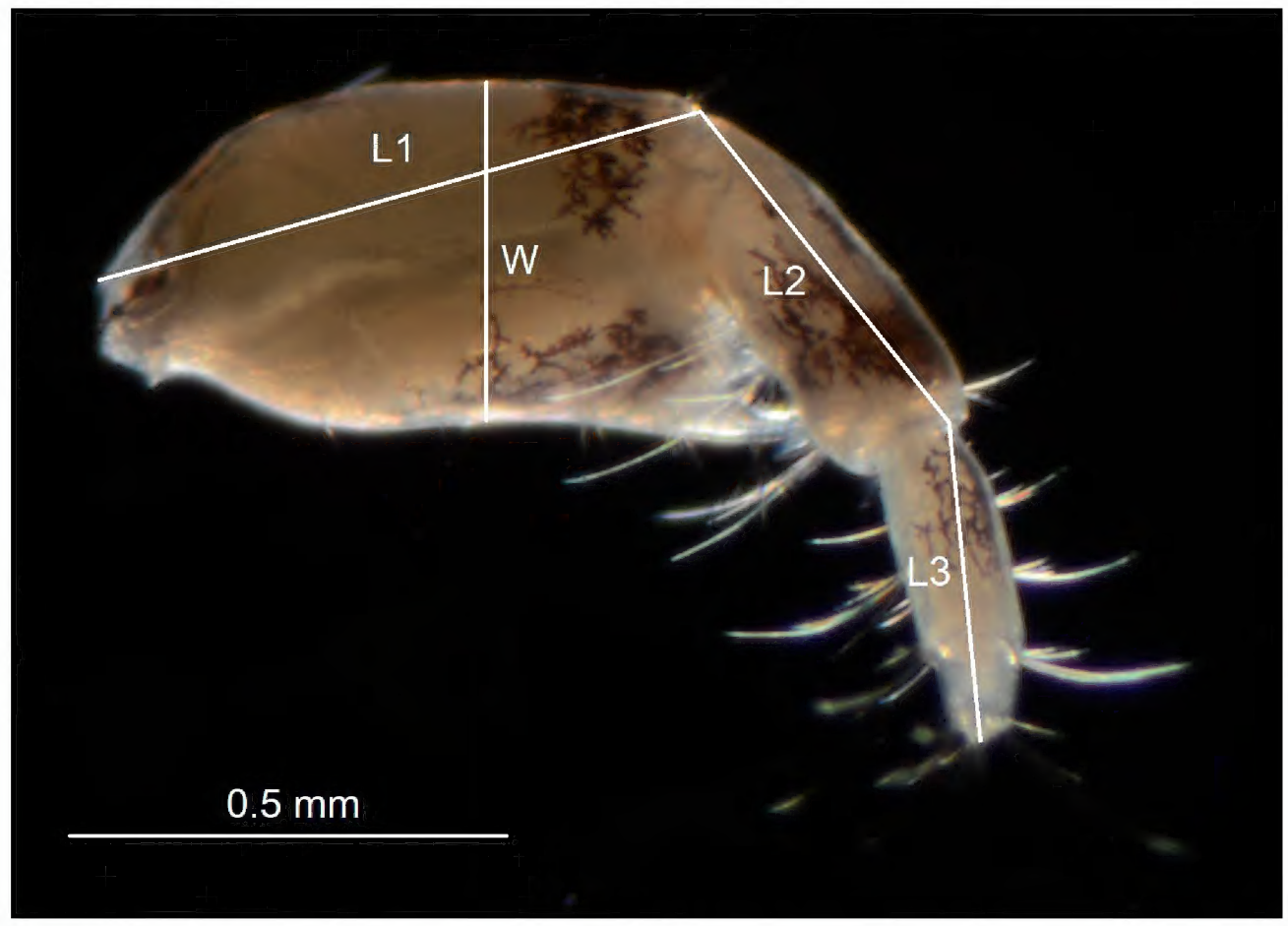

Figure 2. Measurements on the second antennae. Abbreviations: L1-L2-L3 = length, W = width.

Due to the obvious sexual dimorphism, interspecific differences in the width and length of the second antennae relative to body length were tested separately in males and females by linear models on log-log transformed data. The initial models included interaction terms with body length among the species, which proved not significant in all cases and were omitted (Suppl. material 1: table S2). Pairwise comparisons between the intercepts of the species were made using the 'emmeans' package (Lenth 2025) with Tukey's correction for comparing a family of four estimates. For the sake of visual comparability, the relative lengths and widths of the antennae (i.e., antenna lengths and widths divided by body length) are shown in Fig. 4. The log-log transformed data are included in Suppl. material 1: fig. S2.

Results

The mean filter mesh sizes ranged between 1.71 and 5.45 μm in the studied *Chelicorophium* specimens from the Netherlands (Fig. 3A). The filter mesh sizes of *C. maeoticum* varied in an intermediate interval among the four species (2.31–3.63 μm), partially overlapping with the range of *C. sowinskyi* (1.71–3.01 μm). *C. curvispinum* and *C. robustum* had the largest filter mesh sizes (3.45–5.26 μm and 3.58–5.45 μm, respectively), largely overlapping with each other but only slightly with *C. maeoticum* (Fig. 3A). The modelling of interspecific variation among the four species indicated that the effect of body size was relatively weak but significant with negligible differences among species (Suppl. material 1: table S1; Fig. 3A). The pairwise comparison of the intercepts showed significant differences between all species pairs except for *C. curvispinum* and *C. robustum* (Table 2).

Although not modelled explicitly, intraspecific differences among sites in the filter mesh sizes of the four species from the Netherlands were minor compared to interspecific differences (Suppl. material 1: fig. S1). The interaction between body size and sex was not significant in any of the species. The effect of sex was significant only in the case of *C. sowinskyi*, whereas the effect of body length was significant in *C. maeoticum*, *C. robustum*, and *C. sowinskyi* (Suppl. material 1: table S1).

In the River Tisza, the mean filter mesh sizes of the studied *C. maeoticum* specimens ranged between 3.16 and 3.66 μm which did not overlap with the range of the co-occurring *C. sowinskyi* population (1.44–2.16 μm; Fig. 3B). The interaction

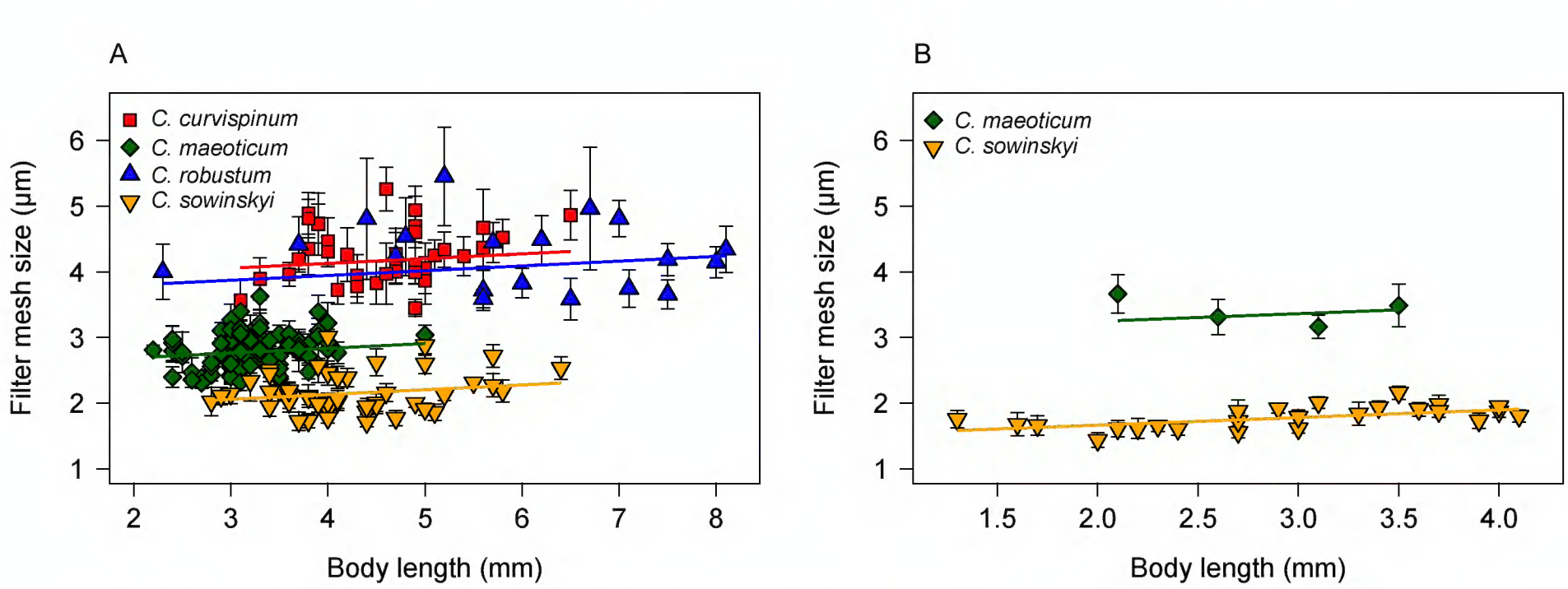

Figure 3. Filter mesh sizes of the studied specimens as a function of their body sizes. **A.** River Rhine; **B.** River Tisza. The regression lines indicate the fixed effects of the optimal interspecific models (Suppl. material 1: table S1). Error bars: ± SD.

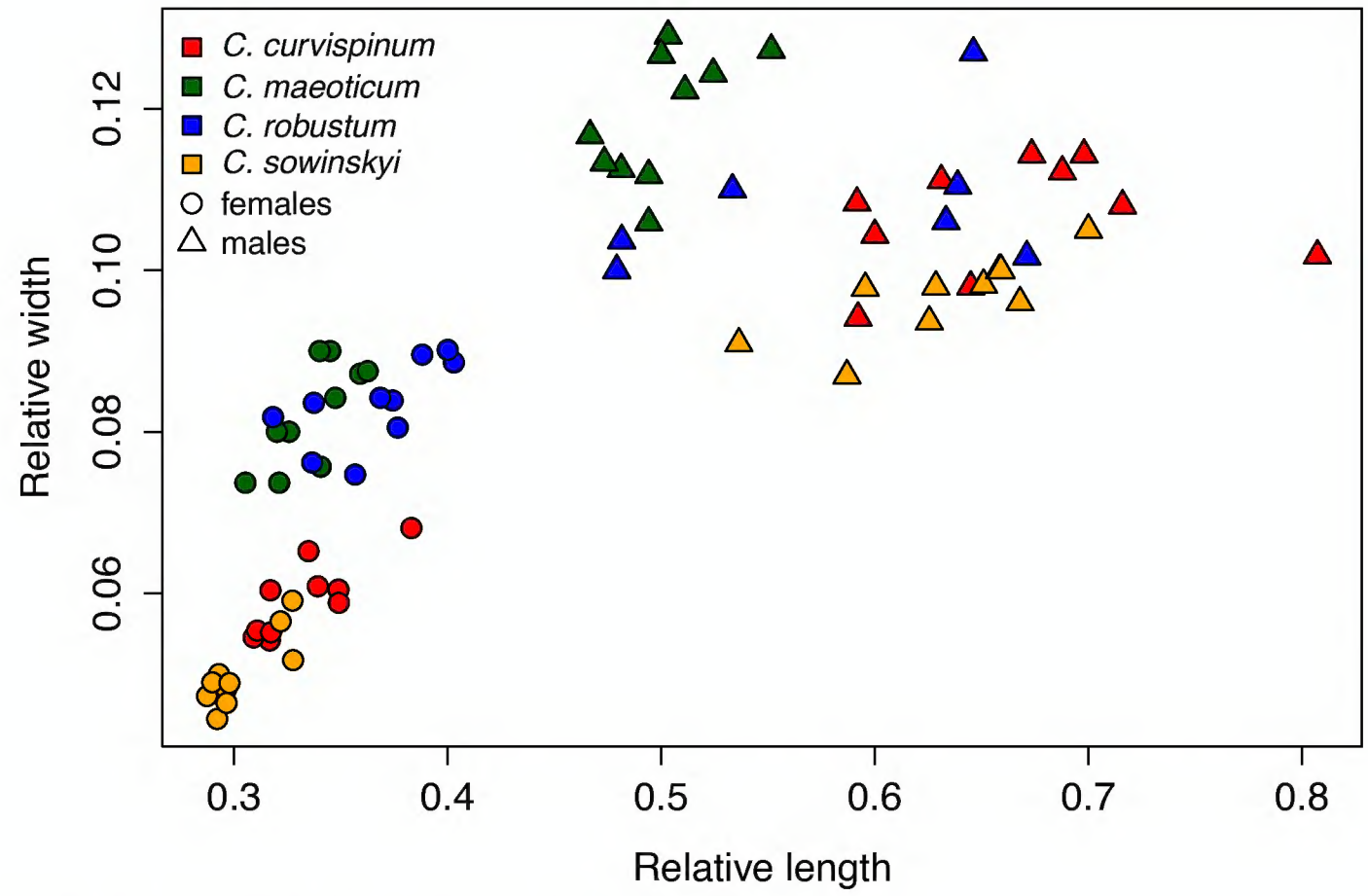

Figure 4. Relative lengths and widths of the second antennae.

Table 2. Pairwise interspecific comparisons of the intercepts (fixed effects) in the linear mixed-effect models of filter mesh sizes in the River Rhine. Abbreviations: CC = *C. curvispinum*, CM = *C. maeoticum*, CR = *C. robustum*, CS = *C. sowinskyi*.

Contrast	Estimate	Std. Error	DF	*t*-ratio	*p*-value
CC–CM	1.292	0.08	167	16.33	< 0.0001***
CC–CR	0.184	0.10	167	1.89	0.2364
CC–CS	1.995	0.08	167	24.56	< 0.0001***
CM–CR	-1.109	0.12	167	-9.47	< 0.0001***
CM–CS	0.703	0.07	167	10.14	< 0.0001***
CR–CS	1.811	0.11	167	16.36	< 0.0001***

of body length between species proved to be negligible during the modelling of intraspecific differences; however, the body length effect was significant (Suppl. material 1: table S1). The difference between the intercepts of the two species was estimated as 1.58 ± 0.08 μm SE (95% CI: 1.41–1.76 μm), significantly higher than in the River Rhine (0.70 ± 0.07 μm SE, 95% CI: 0.52–0.88 μm).

Interspecific differences in the relative length and width of the second antennae were apparent in both sexes (Fig. 4). In females, differences in relative widths were more pronounced than in relative lengths, as *C. maeoticum* and *C. robustum* had considerably thicker second antennae than the other two species, while the relative lengths largely overlapped among the four species (Fig. 4). Pairwise comparisons among the intercepts of the linear models (log-log transformed data) showed significant differences between all species pairs in width, but only between *C. curvispinum* and *C. robustum*, *C. curvispinum* and *C. sowinskyi*, as well as between *C. robustum* and *C. sowinskyi* in length (Table 3).

In males, interspecific differences in the relative lengths of the second antennae were more prevalent than in relative width, although intraspecific variation was high (Fig. 4). *C. maeoticum* males had considerably shorter and also somewhat thicker second antennae relative to its body length than the other three species,

which overlapped with each other largely in both dimensions. In length, pairwise differences among the intercepts of the linear models (log-log transformed data) were significant between *C. curvispinum* and *C. robustum* as well as between *C. robustum* and *C. sowinskyi* (Table 3, Suppl. material 1: fig. S2). In width, pairwise differences were significant between *C. sowinskyi* and all the other species (Table 3, Suppl. material 1: fig. S2).

The maximal body lengths of the species in the studied material were 5, 6.4, 6.5, and 8.1 mm in *C. maeoticum*, *C. sowinskyi*, *C. curvispinum*, and *C. robustum*, respectively. The resulting body length ratios are shown in Table 4.

Discussion

Our results revealed significant differences among the species in all measured parameters, suggesting that multiple mechanisms might be involved in their coexistence.

The filter mesh size of *C. maeoticum* differed significantly from that of the other three *Chelicorophium* species in the River Rhine. However, the filter mesh size range of the newcomer fell within the range covered by the earlier invaders, resulting in a relatively densely packed niche space. In fact, the overall filter mesh size range of the four species can be regarded as relatively narrow considering their adaptive capacity. *C. curvispinum* can have considerably larger filter mesh sizes (up to > 8 μm,

Table 3. Pairwise comparisons of intercepts in the linear models of second antenna length and width as a function of body length (log-log transformed) in females and in males in the four *Chelicorophium* species. Abbreviations: CC = *C. curvispinum*, CM = *C. maeoticum*, CR = *C. robustum*, CS = *C. sowinskyi*.

Trait	Sex	Contrast	Estimate	Std. Error	DF	*t*-ratio	*p*-value
Length	Females	CC–CM	0.033	0.042	35	0.784	0.8613
		CC–CR	-0.142	0.043	35	-3.318	0.0109*
		CC–CS	0.088	0.028	35	3.108	0.0186*
		CM–CR	-0.175	0.070	35	-2.515	0.0749
		CM–CS	0.055	0.045	35	1.239	0.6065
		CR–CS	0.230	0.041	35	5.657	< 0.0001***
	Males	CC–CM	0.143	0.076	32	1.894	0.2509
		CC–CR	0.201	0.054	32	3.732	0.0039**
		CC–CS	0.038	0.040	32	0.936	0.7861
		CM–CR	0.058	0.105	32	0.550	0.9459
		CM–CS	-0.105	0.071	32	-1.486	0.4573
		CR–CS	-0.163	0.057	32	-2.852	0.036*
Width	Females	CC–CM	-0.225	0.047	35	-4.742	0.0002***
		CC–CR	-0.444	0.048	35	-9.275	< 0.0001***
		CC–CS	0.160	0.032	35	5.015	0.0001***
		CM–CR	-0.219	0.078	35	-2.808	0.0387*
		CM–CS	0.384	0.050	35	7.720	< 0.0001***
		CR–CS	0.603	0.046	35	13.246	< 0.0001***
	Males	CC–CM	-0.064	0.056	32	-1.143	0.6663
		CC–CR	-0.037	0.040	32	-0.930	0.7888
		CC–CS	0.102	0.030	32	3.395	0.0095**
		CM–CR	0.027	0.078	32	0.347	0.9854
		CM–CS	0.166	0.053	32	3.147	0.0178*
		CR–CS	0.139	0.043	32	3.269	0.0131*

Table 4. Body length ratios of the species based on their maximal body lengths in the studied material. Abbreviations: CC = *C. curvispinum*, CM = *C. maeoticum*, CR = *C. robustum*, CS = *C. sowinskyi*.

	CR	CC	CS
CM	1.62	1.3	1.28
CS	1.27	1.02	
CC	1.25		

although values exceeding ~6 µm were recorded relatively rarely; Borza 2021), and *C. sowinskyi* can also have smaller filter mesh sizes than observed in the River Rhine (down to ~1 µm; Borza 2021). Overall, the filter mesh sizes of *C. sowinskyi* are even somewhat larger than usual for the species, while those of *C. curvispinum* and *C. robustum* show a good match with the most frequently recorded values (Borza 2021). Accordingly, it seems unlikely that the observed filter mesh sizes of the three earlier invaders shifted in response to the appearance of the new competitor.

C. maeoticum showed the strongest niche overlap with *C. sowinskyi*. The estimated 0.7 µm mean difference between the two species in the River Rhine is considerably smaller than in the River Tisza (1.58 µm) and also smaller than between *C. robustum* and *C. sowinskyi* in the Lower Danube (1.37 µm; Borza et al. 2018a). However, even more surprising is the 0.7 µm overlap in the filter mesh size ranges of the two species, since this is the first time that an overlap is reported for *C. sowinskyi* with any other species. Accordingly, niche differentiation by food particle size alone might not guarantee the stable coexistence of these two species. On the contrary, the estimated 1.1–1.3 µm mean difference and relatively small overlap between *C. maeoticum* and *C. curvispinum*/*C. robustum* is comparable to the differentiation among the three *Chelicorophium* species in the Lower Danube (Borza et al. 2018a). The almost complete lack of differentiation between *C. curvispinum* and *C. robustum* is quite puzzling and could be interpreted as a tension created by the appearance of a new invader. However, previous studies have demonstrated that such strong overlaps between the filter mesh sizes of these two species can occur even in the absence of other congeneric competitors, suggesting factors other than food particle size might also contribute to their niche differentiation (Borza 2021).

The present study confirmed the notion that the food particle size spectrum can be divided only into three partitions by corophiids even if more than three species are present. Nevertheless, it is surprising that the species apparently did not exploit their full capacity to differentiate. The reason for this might lie in the environmental conditions, i.e. the narrow size distribution of food particles or the presence of other filter feeding competitors might act as a selection pressure against differentiation. In light of the relatively recent invasion of *C. maeoticum*, we also have to consider the possibility that the other species have not had enough time to shift their niches in response to the invader. Alternatively, it is also conceivable that the population densities of the *Chelicorophium* species are kept low by predators or by the scarcity of predator-free microhabitats, implying that the intensity of competition for food is low.

Our measurements indicated interspecific differences in the relative length and width of the second antennae in both sexes, suggesting that it might have functions beyond sexual competition, potentially contributing to the niche differentiation of the species. Being sedentary animals, intra- and interspecific competition for space is expected to take place among corophiids when habitat availability limits their population growth. Based on the apparent advantage of larger males in fights

over females in *C. volutator*, Jensen and Kristensen (1990) suggested that the larger body size of *C. volutator* might make it dominant over *C. arenarium* in territorial competition. These species live in U-shaped burrows with flexible walls in mud which can accommodate different sized animals within certain limits. By contrast, we hypothesize that competition within and among *Chelicorophium* species might be strongest between similar sized specimens, since crevice size limits the body size of the occupants in their microhabitats. Accordingly, success in combats might be determined primarily by properties of the second antennae rather than body size. Judging by the both longer and thicker antennae of males, we expect that both dimensions are important in this regard. In females, however, further increasing the length of the antennae would likely come at a cost in brood size. Based on their thicker antennae in both sexes, *C. maeoticum* and *C. robustum* appear to be dominant in interference competition, whereas *C. curvispinum* and *C. sowinskyi* can invest more in somatic growth and reproduction. Remarkably, the latter two species had higher success in colonizing new areas, while *C. maeoticum* and *C. robustum* could establish in habitats already occupied by their congeners. A similar pattern can be observed in *Dikerogammarus* species, where the gracile and faster-spreading *D. haemobaphes* (Eichwald, 1841) is often replaced by the more robust and competitively superior *D. villosus* (Sowinsky, 1894) (Kobak et al. 2016).

Deposit feeding is another potential function of the second antennae which could contribute to the niche differentiation of corophiids; however, its relevance for the invasive Ponto-Caspian species is dubious at this point. Due to their different habitats, it seems unlikely that the invasive *Chelicorophium* species would use their second antennae for scraping surfaces in the same manner as described in *C. volutator* (Meadows and Reid 1966; Riisgård and Schotge 2007). They can be expected to eat everything they can salvage around their tubes if suspended food particles are scarce, in which the length of the second antennae might be important. However, differentiation in this regard was low among females, and variability was high in males. Therefore, even if the species feed on deposit under certain conditions, it might not be relevant to their coexistence if the species do not differ in their efficiency.

The body length ratios of the species are remarkably close to 1.3, which is often reported between guild members in various organisms and regarded as the minimal size difference allowing coexistence (Hutchinson 1959). A similar ratio was also reported between *C. volutator* and *C. arenarium* (Jensen and Kristensen 1990). While the generality of 'Hutchinson's Rule' is debated (Eadie et al. 1987), body size differences can evidently contribute to the niche differentiation of species in various ways. Although food particle size in corophiids is determined by filter mesh size rather than the size of mouthparts, body size-related differences in e.g., life history, microhabitat use, or predation risk can be assumed to play a role in their coexistence.

Overall, filter mesh size, body length, and provisionally also the relative width of the second antennae can be regarded as proxies of independent niche axes which can contribute to the coexistence of the species under various selection regimes. Previous studies suggested a non-random association in the positions of the species along the niche axes minimizing overall niche overlap in accordance with evolutionary theory (Ashby et al. 2017; Borza et al. 2021a).

There are signs of such associations also in the present case, since *C. curvispinum* and *C. sowinskyi* with similar body sizes are the most different in filter mesh sizes,

while *C. maeoticum* and *C. robustum* with the largest difference in body size have similar second antennae. Nevertheless, testing for such patterns should be done in a phylogenetic context involving all Ponto-Caspian *Chelicorophium* species, allowing the detection of potential phylogenetic signals in the traits (i.e., niche conservativism).

Conclusion

Our study revealed differentiation among the invasive Ponto-Caspian *Chelicorophium* species in multiple aspects, which might allow their coexistence. Accordingly, we expect the species to persist in their invaded ranges, although their abundances might change over time. The continued spread of *C. maeoticum* should also be anticipated in the interconnected waterways of Western and Central Europe in contrast with its previous decline in the Danube catchment, which seems even more enigmatic in light of our results. Based on their apparently smooth coexistence in the River Rhine, it seems less likely that the decline of *C. maeoticum* in the Danube catchment was caused by the appearance of *C. curvispinum*, as hypothesized by Borza et al. (2015). Instead, differences in the local conditions or between the two populations can be assumed. The latter might potentially include changes linked to the invasion process, such as microevolutionary adaptations or enemy release. Our results on the likely role of the second antennae in the niche differentiation of the species provide a novel perspective on their ecological interactions beyond food resource partitioning. Nevertheless, more studies are needed to reveal the range of behaviors these peculiar appendages are involved in and how their morphological features determine their functionality.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
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Data availability

All of the data that support the findings of this study are available at https://doi.org/10.6084/m9.figshare.30104323

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Supplementary material 1

Supplementary figures and tables

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Data type: pdf

Explanation note: **figure S1.** Filter mesh sizes of the studied specimens from the River Rhine as a function of their body sizes by sites. **figure S2.** Second antenna length and width in females and males as a function of body length (log-log transformed). **table S1.** Parameters (fixed effects) of the inter- and intraspecific linear mixed-effect models of filter mesh sizes. **table S2.** Parameters of the linear models of second antenna length and width in females and in males in the four *Chelicorophium* species.

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